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# Speciation and evolution in the Soricidae (Mammalia: Insectivora) in relation with the paleoclimate <sup>1</sup>

by

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With 1 figure

## ABSTRACT

An attempt is made to correlate the history of the paleoclimate to the evolutionary history of the Soricidae. Therefore, the evolutionary history and the ecophysiology of the family are briefly outlined. It is concluded that the factors temperature and humidity play a crucial role in the ecology of shrews. It is thus conceivable that the evolutionary history of the family Soricidae is influenced by climatic changes. It is supposed that the climatic (cooling and desiccating) event around the Miocene/Pliocene boundary is responsible for the extinction of the subfamily Crocidosoricinae. The Soricinae exploited the then vacant positions, and strongly radiated during the Pliocene. Then, the cooling event around the Pliocene/Pleistocene boundary caused a severe decrease in Soricinae diversity. The subsequent Pleistocene climatic fluctuations caused several recorded speciations, migrations and extinctions to occur. The Holocene climatic amelioration, finally, supports a new speciation in the genus *Sorex*.

## INTRODUCTION

Soricidae, or shrews, have been forming part of the European mammal fauna since the middle Oligocene, which implies a time-span of roughly 30 million years (My). Their

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overall appearance has not changed much during this long period: shrews were and are small to very small mammals, with a characteristic dentition showing large incisors and dilambdodont upper molars.

This paper is a first attempt to combine what is known about the evolutionary history of the Soricidae with present knowledge of the ecophysiology of the family and of paleoclimatic events. REPENNING (1967), JAMMOT (1983), REUMER (1984 and 1987) reviewed the family's evolution, which is now *grosso modo* known. Three major paleoclimatic events will be considered in combination with this evolutionary knowledge: the cooling and desiccating event around the Miocene/Pliocene boundary, the cooling event around the Pliocene/Pleistocene boundary, and the Pleistocene glaciations and subsequent Holocene warming.

## MAJOR EVOLUTIONARY EVENTS IN THE SORICIDAE

### A. THE ORIGIN OF THE FAMILY

The oldest true soricid yet known is *Srinitium marteli* Hugueney, 1976. It could be dated to the middle Oligocene (roughly 30 My).

It is not exactly known where the Soricidae originated from, but several morphological features point towards the Nyctitheriidae, a family common in Paleogene associations (SIGÉ 1976). Whatever the exact relationship between the Nyctitheriidae and the Soricidae, the Oligocene is marked by the presence of two parallel developments: the emergences of the families Soricidae and Heterosoricidae (the latter was included in the former until recently, REUMER 1987). Only the Soricidae in the present *sensu stricto* definition will be considered in this paper.

It is, finally, worth mentioning that the early Oligocene "Grande Coupure" (a major paleo-biogeographical event marked by numerous extinctions, next to the introduction of mainly Asiatic faunal elements) postdates the extinction of the Nyctitheriidae and predates the first known appearance of the Soricidae in Europe (SIGÉ 1976; see also figure 1).

### B. FOUR DIFFERENT SUBFAMILIES

*Srinitium marteli* and many other Oligocene and Miocene shrews belonged to the subfamily Crocidosoricinae (see REUMER 1987, for a diagnosis). The Crocidosoricinae lived on till the latest Miocene. A possible survivor into the earliest Pliocene occurred on the Italian island (now peninsula) of Gargano (see DE GIULI *et al.* 1987), but apart from this exception it can be stated that the subfamily did not survive beyond the Miocene/Pliocene boundary.

In the Miocene, the Crocidosoricinae gave rise to three other subfamilies: the now extinct Limnoecinae Repenning, 1967, the Soricinae Fischer von Waldheim, 1817, and the Crocidurinae Milne-Edwards, 1868-1874; both latter taxa still occur. See REUMER (1987) for morphological details about the developments of these three subfamilies.

The Limnoecinae were a development restricted to North America (REPENNING 1967), where they appeared to somewhat parallel the Old World Crocidurinae in several morphological aspects. Limnoecinae occurred from the early Miocene up till the middle Pliocene (figure 1).

The Soricinae occur in North America and Eurasia. The oldest true Soricinae so far recorded appears to be *Paenelimnoecus crouzei* Baudelot, 1972 from the middle Miocene of Sansan, France. In Europe, Soricinae bloomed during the Pliocene (indicated by the wider bar in figure 1), followed by a dramatic decline around the Pliocene/Pleistocene boundary (REUMER 1985). The most abundant genus nowadays is *Sorex*, which has many species both in Eurasia and in North America. Yet many other genera are known both as fossils and living. The diversity among them has led to the distinction of seven tribes (see REUMER 1984 for details).

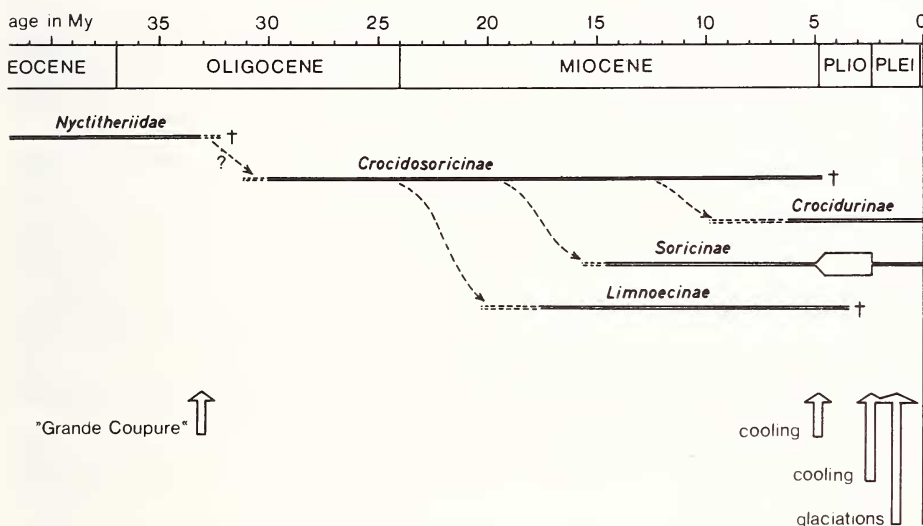


FIGURE 1.

Chart showing the relationship between the Nyctitheriidae, the four subfamilies of Soricidae, and the absolute time-scale (given at the top in millions of years, My). Also indicated are the Oligocene "Grande Coupure" and the three climatic events that are discussed in the text: the cooling/desiccating event around the Miocene/Pliocene boundary, the cooling event around the Pliocene/Pleistocene boundary, and the Pleistocene glaciations. The wider part in the bar of the Soricinae indicates the sub-family's flourishing during the Pliocene.

The Crocidurinae, finally, abound mainly in Africa, but are also found in Europe and Asia. The fossil record of the Crocidurinae is very incomplete; a late Miocene record from Kenya so far seems to be the oldest (see REPENNING 1967).

Figure 1 depicts the evolutionary relationships between the four subfamilies (and the Nyctitheriidae), plotted alongside a time-scale. In it, several important paleoecological events are indicated next to the "Grande Coupure": the cooling and desiccating event around the Miocene/Pliocene boundary, the cooling event around the Pliocene/Pleistocene boundary and the Pleistocene glaciations. We will consider these three events, after a short look at the ecophysiology of shrews.

## THE ECOPHYSIOLOGY OF SHREWS

Soricidae are small to very small mammals. Several species are at or near the size limit for homoiothermic animals, which implies a high metabolic rate. VOGEL (1980) gave an extensive overview of the ecophysiology (metabolic levels and biological strategies) of shrews.

The two living subfamilies, Soricinae and Crocidurinae, differ in their energy metabolism. The metabolic level is higher in the Soricinae (VOGEL 1980). The reason for this divergence in metabolic levels is most likely due to the different regions where the two subfamilies originated and/or evolved: the Soricinae in the Holarctic region, the Crocidurinae in the Paleotropics.

There apparently exists a mutual relationship between the biogeography of a certain group (subfamily, genus) and its metabolism. One influences the other. This explains why, in Europe, Crocidurinae ("cold shrews" in the words of VOGEL 1980) are not found North of about 53 degrees latitude, while Soricinae ("hot shrews") can be found as far North as Finland.

In an earlier paper (REUMER 1985) the importance was stressed of (paleo) temperature in determining soricid abundance and/or diversity. Although temperature will certainly have its influence, it appears that moisture is no less crucial: a cooler and moister environment likely favours shrews, while a cooler and drier climate might have an adverse effect (KIRKLAND, *in litt.*). It is important to understand in this context that a warming, with a constant amount of moisture, leads to a drop in relative humidity, so that a temperature change is likely to also influence animals that are critical in their humidity range.

With this knowledge in mind, we will look at some paleoclimatic events and their possible influence on soricid development.

## THE CLIMATIC EVENT AROUND THE MIOCENE/PLIOCENE BOUNDARY

The Miocene/Pliocene (M/P) boundary is dated at 4.83-4.84 My (ZIJDERVELD *et al.* 1986). However, literature data often mention older dates: up till 5.4 My. In the framework of this article, the M/P boundary is considered to more or less accurately correlate with the Messinian/Zanclean boundary (in the Tethan marine stratigraphy) and the Turolian/Ruscinian boundary (in the European continental stratigraphy); see e.g. BERGGREN (1985: 32).

The available literature is not in extreme consensus about the exact nature of the climatic events around the M/P boundary. A selection of literature sources will be cited here.

BARKER *et al.* (1987) correlate sedimentary events at about 5.3 My in the Weddell Sea to an expanding West Antarctic ice sheet; by 4.8 My this ice sheet appeared to have become a permanent, stable feature. CHEPALYGA (1985) noted an arid and cold phase at the M/P boundary in the Paratethys. In the Mediterranean, a cooling event is marked by the entry of sub-polar planktonic foraminifera (*Globorotalia conomiozea* group, see ZACHARIASSE 1982). DERMITZAKIS & GEORGIADES-DIKEOULIA (1987) mention an impoverishment of the marine mollusc fauna in a zone which they correlate with the *G. conomiozea* zone. DEMARCO (1987: fig. 1) notes an intense cooling trend which begins

at the end of the Messinian and which continues into the Pliocene. MOISETTE & POUYET (1987) explain the modifications in bryozoan faunas of the Mediterranean by cooling. A well developed picture of the Miocene and Pliocene climatic history is given by VANDER ZWAAN & GUDJONSSON (1986). They reported several coolings, of which the one at 5.6-4 My is regarded to be a minor one. SPAAK (1983) mentions the apparent presence of distinctly cooler conditions at higher latitudes by the Late Miocene. This apparently suggests a certain geographical differentiation. Also, the cooling trend seems to have gone together with a desiccation. In the marine record, this desiccation led to the so-called Messinian salinity crisis (the drying out of the Mediterranean due to climatic changes and sea-level lowering). However, also students of continental fossils mention a desiccation at the end of the Miocene; KORDOS *et al.* (1987) are an example.

It is not improbable that the cooling event was best noted at higher latitudes. The formations of ice-sheets at high latitudes are well documented, but on the other hand LOPEZ-MARTINEZ *et al.* (1987) failed to show a cooling phase at the Turolian/Ruscinian boundary in the Spanish continental sequences.

Figure 1 shows the disappearance of the Crocidosoricinae around the M/P boundary. It is here supposed that this extinction might be correlated with the cooling and desiccating event mentioned above. Although climatic fluctuations occurred at several periods during the Oligocene and Miocene (CHEPALYGA 1985; LOPEZ-MARTINEZ *et al.* 1987), the drop in temperature that was achieved around the M/P boundary appeared to have been the severest that far (CHEPALYGA 1985).

The mentioned survival into the Pliocene of a Crocidosoricinae as a relict on the Italian island of Gargano does not falsify this hypothesis. It is conceivable that the cooling event caused a retreat of shrews into more southern latitudes; similar migrations were observed during the Pleistocene (REUMER 1984, and below).

The extinction of the Crocidosoricinae left an ecologically underexploited Europe when the climatic situation ameliorated during the Pliocene (Ruscinian). This explains the radiation shown by the Soricinae during this period (REUMER 1984, 1985, and indicated in figure 1 by the wider bar).

## THE COOLING AROUND THE PLIOCENE/PLEISTOCENE BOUNDARY

As with the M/P boundary, the Pliocene/Pleistocene (P/P) boundary causes disputes as to its age. Estimates vary between 1.6 My (TAUXE *et al.* 1983) and ca. 2.4 My (DRIEVER 1984). In the framework of the present article, the P/P boundary is considered to more or less accurately correlate to the Ruscinian/Villányian boundary (mammal stages), the Reuverian/Praetiglian boundary (Northwest European stages), and the Mediterranean pollen zones boundary P II/P III (see REUMER 1985). We thus speak of an age of about 2.4-2.5 My.

An intense cooling episode at this period is well documented. Based on pollen samples from the Netherlands, SUC & ZAGWIJN (1983) noted the first occurrence of tundra-like vegetation in the Praetiglian, the base of which they placed at about 2.3 My. A similar cooling indicated by a French pollen flora was dated at about 2.5 My (*ibid.*). Other examples are to be found in DRIEVER (1984: calcareous nannofossils), SPAAK (1983: planktonic foraminifera), ZACHARIASSE & SPAAK (1983: *idem*), BONNEFILLE (1983: pollen), SHACKLETON *et al.* (1984: North Atlantic ice rafting), and REA & SCHRADER (1985: North Pacific ice rafting). In at least one reference also a desiccation of the climate was noted (BONNEFILLE 1983).



The fate of the European shrew fauna during the late Pliocene — early Pleistocene is well documented (REUMER 1984, 1985). The Ruscinian shrew faunules are often very rich in species. Already in the early Ruscinian localities we can find 6-8 species, whereas in the late Ruscinian ones a number of species well above 10 is not unusual: the Polish locality of Węże 1 yielded 13 species, the Hungarian locality of Csarnóta 2 contained 12 species, and Osztramos 7 even 15 species.

The subsequent Villányian faunas are much poorer in the composition of the shrew assemblages: Beremend 5 and 11 (Hungary) both contain only 4 species, as does Tegelen (the Netherlands). Rebielice Krolewskie (Poland) contains 5 species, Villány 3 (Hungary) 6, and Osztramos 3/2 (also from Hungary) yielded 5 species (KOWALSKI 1960; SULIMSKI 1962; JÁNOSSY 1979; SULIMSKI *et al.* 1979; REUMER 1984). This general picture does not change in the Biharian (the stage following the Villányian).

Summarizing, a considerable impoverishment of the Soricidae occurred at the Ruscinian/Villányian boundary in Europe. Not only did the diversity diminish, many of the taxa involved became extinct. All of the shrew taxa that lived in Europe during the Pliocene (Ruscinian), were members of the subfamily Soricinae. Apparently the Pliocene paleoenvironment favoured a radiation and diversification, but then the onset of the glaciations with cooler and probably drier conditions by 2.4 My caused a strong decline (REUMER 1985).

## THE PLEISTOCENE GLACIATIONS AND THE HOLOCENE

Finally, we will look at the developments of the European shrew fauna during the Quaternary: the period comprising the Pleistocene and Holocene. Broadly speaking, the Pleistocene is characterized by a sequence of cooler and warmer periods, glacials and interglacials, although the real picture is much more complicated than this.

As with many other groups of animals and plants, the shrews were strongly influenced by the climatic situation. As we will see, the Pleistocene soricid developments show rapid speciations, migrations and extinctions.

The sharp decline of Soricinae around the P/P boundary should theoretically have led to a situation in which new developments could occur due to the many void ecological niches. This was hampered by the relatively quick succession of climatically severe periods. Yet the relatively warmer and/or moister climate of the various climatic intervals allowed some interesting developments to occur.

First, the existence of at least two aberrant, short-lived, genera of Soricinae is worth mentioning: *Macroneomys* and *Dimylosorex*. *M. brachygnathus*, a large shrew related to the water-shrews (tribe Soriculini), was described by FEJFAR (1966) from Zlatý Kun (Czechoslovakia); it was also found (but not yet described) in Kövesvár (Hungary, JÁNOSSY 1963) and in les Abîmes de la Fage (France, JAMMOT 1975). Its stratigraphical range seems restricted to the middle or late Biharian. JAMMOT (1975) concluded the faunule from which his *Macroneomys* originated to have had a moist characteristic.

*Dimylosorex tholodus* was described by RABEDER (1972) from the early Biharian (Betfia-phase) of Deutsch-Altenburg 2 in Austria. As far as known, the taxon has not been found elsewhere yet. RABEDER (*l. c.*) pointed out that *Dimylosorex* was a malacophagous

(snail-eating) animal, as shown by its strongly exoedaeodont ("bulbous") dentition. Knowing the habit of snails to be predominantly active — and thus capturable — at moist conditions, it may be inferred that *Dimylosorex* preferred a moist environment. Since the Biharian is a generally cooler period, this stresses the above-mentioned crucial role moisture plays in soricid ecology and evolution.

With the changes in climate, the different vegetational zones in Europe moved north and south. This was evidently accompanied by migrations of the fauna. REUMER (1984) recorded two of such migrations.

The first one is the northward advance of the genus *Crocidura*, followed by a southward retreat after the Eemian/Ipswichian interglacial. Starting in Asia Minor during the late Ruscinian (VAN DE WEERD *et al.*, 1982), *Crocidura* advanced northward, to reach Greece by the early Villányian (REUMER & DOUKAS 1985), Hungary by the late Villányian (REUMER 1984), and finally England by the Eemian/Ipswichian (RZEBIK 1968; STUART 1976). The onset of the Weichselian glaciation apparently caused a (southward) retreat from England; nowadays the genus is absent from Britain (even though the southern part of England has a favourable climate, but the opening of the Channel so far blocked a re-invasion; REUMER 1984).

The second climate-induced migration concerns the soriculine genus *Episoriculus*. During the Ruscinian, *Episoriculus gibberodon* was widespread in Europe, from as far north as Poland to Asia Minor (REUMER 1984). The youngest record in Poland dates from the early Ruscinian (Podlesice; RZEBIK-KOWALSKA 1981); in the Hungarian/Czechoslovakian region, the species persisted until the early Biharian (e.g. Osztromos 14; JÁNOSSY 1979). *Episoriculus castellarini* is found in several middle Biharian Italian localities (e.g. Monte Peglia; VAN DER MEULEN 1973). The genus finally continued to survive into the Holocene on four Mediterranean islands as the subgenus *Episoriculus* (*Nesiotites*) (see REUMER 1984). It then became entirely extinct in Europe. The situation seems to resemble that of the subfamily Crocidosoricinae, that became extinct around the Miocene/Pliocene boundary, but that had a possible survivor on the Italian island of Gargano.

A third example of climate-induced migration was inferred by CATZEFLIS (1984). He supposed that *Crocidura suaveolens* invaded Europe and the surroundings of the Mediterranean basin during the Riss-Würm interglacial (=Eemian), and that the species was subsequently forced into three refuge areas during the subsequent Würm glacial (=Weichselian): the south of Italy, the south of the Balkan, and Asia Minor (CATZEFLIS 1984: figure 70.3). The three thus separated populations somewhat diverged during their isolation, and in this way CATZEFLIS explained the morphological and biochemical polymorphism that is found in living *C. suaveolens*. It could be considered an example of primarily climate-induced speciation.

Since the end of the Pleistocene, a relatively warm and humid climate prevails in Europe. This should, in analogy to the situation at the beginning of the Pliocene and during the less severe Pleistocene intervals, set the stage for new speciations.

This is indeed the case. The genus *Sorex* shows an intricate pattern of cytogenetically (REUMER & MEYLAN 1986) and biochemically distinct species or "races". Several of the species belonging to the *araneus-arcticus* group, especially *S. araneus* and *S. tundrensis*, show a cytotaxonomical polymorphism that can be explained as a speciation process "in action" (e.g.: HAUSSER *et al.* 1986).

## CONCLUSIONS

The factors temperature and humidity play a crucial role in the ecology of shrews. It is thus conceivable that the evolutionary history of the family Soricidae is influenced by (strong) changes in climate. It is supposed that the climatic (cooling and desiccating) event around the Miocene/Pliocene boundary is responsible for the extinction of the sub-family Crocidosoricinae. The Soricinae exploited the then vacant positions, and flourished during the Pliocene. Then, the cooling event around the Pliocene/Pleistocene boundary caused a severe decrease in Soricinae diversity. The subsequent Pleistocene climatic fluctuations caused several recorded speciations, migrations and extinctions to occur. The Holocene climatic amelioration, finally, allows a new speciation in the genus *Sorex*.

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